Bacterial populations of litter and soil in a deciduous woodland

II. — Numbers, biomass and growth rates

BY

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INTRODUCTION

HISSETT and GRAY (1973) have described the principle types of aerobic heterotrophic bacteria that could be isolated from the soil and decomposing litter in Meathop Wood, Lancashire, England. Using these data, together with estimates of the numbers of bacteria present in these environments, it is possible to calculate the biomass of the whole bacterial population and the different types of organism, and to calculate the maximum growth rates that such organisms could achieve in nature.

BABIUK and PAUL (1970) attempted to work out growth rates for bacteria in a grassland soil from their data on energy input and bacterial numbers measured by a direct observation technique. They pointed out that direct counts of bacteria include dead and living bacteria and thus overestimate the biomass. We have used a dilution plate technique to count the organisms, which will underestimate the biomass but does ensure that only living organisms are counted. These data, together with measurements of the cell weights of the main types of bacteria found in this woodland are presented in this paper.

MATERIALS AND METHODS

Sampling and counting procedure: Dilution plate counts were made of bacteria on two representative litter types, i.e. *Quercus petraea/Q. robur* x *petraea*, an

Reçu le 15-XII-72.

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example of slowly decaying litter, and *Fraxinus exelsior*, a rapidly decaying litter. Leaf litter, collected in hammocks placed under the trees in the autumn, was air dried in an unheated room. The dried litter was placed in nylon nets (mesh size c. lcm., BOCOCK and GILBERT, 1957) which were then placed on the soil surface. This procedure enabled the experimental litter to be identified without restricting access for the normal litter fauna. The nets were placed on the soil surface in early November and were sampled at intervals by placing one or more nets in unsealed polythene bags and taking them back to the laboratory at 4° where they were kept overnight before counting.

Dilution plate counts were also made of bacteria in the amorphous humus layer found on the soil surface ($A_h + O_h$ layer) and at various depths in the mineral soils. A block of soil, approximately 15 cm × 15 cm × 15 cm was cut with a spade and transported to the laboratory at 4° and kept overnight. Sub-samples were then taken from the interior of the block, which included fine roots.

The dilution plates of both litter and soil bacteria were prepared as described by HISSETT and GRAY (1973). Eight replicate plates were prepared at each dilution and the colonies counted after 14 days incubation at 25°.

Determination of cell dry weights: In order to determine the bacterial biomass for the ecosystem, the mean cell dry weight was determined for representatives of each taxonomic cluster of isolates (HISSETT and GRAY, 1974). Cultures for dry weight measurement were grown in filtered nutrient broth + 10 % (w/v) glucose on an orbital shaker for 30-100 hr at 25°, until near-maximum yields were obtained. Portions of the broth culture were centrifuged, washed and the pellet resuspended in 4ml deionised water. A sub-sample of the resultant heavy suspension was preserved with formaldehyde and used for a cell count, using a Helber counting chamber (Hawksley Ltd., London). Samples (0.5 ml) from the remainder of the cell suspension were placed in dry, tared lyophilization tubes and vacuum dried over phosphorus pentoxide overnight on a centrifugal freeze dryer (Speedivac, Edwards High Vacuum Ltd., Crawley, Sussex). The final pressure reached was about 0.04 torr. Dried tubes were weighed immediately after removal from the freeze-dryer. This weight and the cell count for the suspension were used to calculate the mean cell weight.

Estimation of biomass: The plate count data obtained during the investigation of seasonal variations in bacterial numbers was used to determine an average value for the biomass of bacteria per gram of the different environments studied. Since the total weight of these environments has also been estimated, it was possible to calculate the total bacterial biomass in the soil ecosystem, using certain assumptions (see below). The biomass of each of the principle groups of bacteria could also be determined since the numbers of bacteria in each taxonomic cluster was a measure of their proportion in the whole population (HISSETT and GRAY, 1973).

Biomass estimates for the litter were based on the average amounts left during. These were 211.1 kg/ha for *Fraxinus* and 971 kg/ha for *Quercus*. The $O_h + A_h$ layer weighed 2.36×10^4 kg/ha and the underlying mineral soil weighed 2.74×10^6 kg/ha (SATCHELL, pers. comm.).

Thus the biomass/hectare for the group and habitat involved can be calculated from the formula

$$B = NMpm$$

where B = biomass/ha for the group and habitat involved, N = average viable bacterial count / g, M = mass/ha of the habitat in grams, p = proportion of the

total isolates from the habitat in the particular taxonomic group and m = cell dry weight for a representative of the taxonomic group.

Unclassified bacteria were assumed to have the same dry weight/volume relationships as the average of the classified organisms. Thus their cell dry weights (m) were calculated from length and breadth measurements of cells and assumed density values.

RESULTS

Variation in bacterial numbers in the humus and mineral soil.

Spatial variation. Nine soil samples were taken from the A_1 horizon, at a depth of 6 cm below the H layer, simultaneously. Three replicate series of dilution plates were prepared for each sample, with eight replicate plates at each dilution. The results are given in Table 1. The standard deviation

TABLE 1

Spatial variation in bacterial numbers in the mineral soil (6 cm depth) Counts expressed in millions per g. oven dry soil

Sample	No. bacteria per g. oven dry soil
1	2.03
2	1.53
3	1.47
4	1.99
5	1.07
6	1.60
7	2.34
8	2.14
9	2.85
Mean	1.89
Standard deviation	0.53

at 28.2 % of the mean is in the range to be expected simply from error in the counting procedure when applied to soil organisms (HISSETT, 1970) and so there is no indication that there are significant differences in population level between different parts of the site in the mineral soil.

Depth. Variations in bacterial count with depth in the soil were estimated by taking three sets of samples at weekly intervals from the soil surface (humus layer) down to bed rock. Two of the profiles examined were between 20 and 30 cm deep, while the third (coinciding with a fissure in the underlying limestone) was 80 cm deep. The counts obtained from these samples are given in Table 2 together with the means and standard deviations

for the 0, 3, 6, 10 and 20 cm depths. Using *d* and *t* tests (BAILEY, 1959), it was found that the means of the counts from the 0 and 6 cm depths were significantly different at the 90 % level of probability but not at the 95 % level. However, there were no significant differences between the 6 and 20 cm depths at either level of probability. It is also clear that the counts obtained from the humus layer are much more variable than those obtained from the mineral soil.

TABLE 2

The effect of soil depth on bacterial numbers
Counts expressed in millions per g. oven dry soil

Depth (cm)	No. of bacteria per g. oven dry soil			Mean with Standard Deviation
	Profile 1	Profile 2	Profile 3	
0	15.3	55.1	14.4	28.27/23.3
3	9.85	6.75	4.63	7.08/2.63
6	4.00	3.48	3.22	3.57/0.80
10	4.9	3.27	1.75	3.31/1.58
20	4.60	5.02	3.65	4.42/0.71
30	Bed rock	1.45	1.59	
40	Bed rock	3.70	Bed rock	
50	Bed rock	2.24	Bed rock	
60	Bed rock	3.76	Bed rock	
70	Bed rock	4.18	Bed rock	
80	Bed rock	5.43	Bed rock	

On the basis of these results it was decided to examine seasonal variations in bacterial numbers in the soil by counting organisms at Ocm and 6 cm depths only.

Seasonal variations. Monthly samples were taken from the humus layer and the mineral soil (6 cm depth) from November 1966 to September 1968. The results for the mineral soil are given in Table 3, together with variations in pH, moisture content, organic carbon content and loss on ignition of the soil samples. The variances for both the 1967 and 1968 counts were significantly greater than those obtained from the data on spatial variation (95 % level of probability). However, there were no clear seasonal trends and the fluctuations in count observed, although significant, do not correlate with any of the soil factors examined, or with changes in temperature. Neither were correlations between these same factors and the variations in numbers of bacteria observed in the humus layer found (Table 4).

Variations in bacterial numbers on leaf litter.

Ash litter. Counts were made on ash litter from the time it was placed on the soil surface to the time it was no longer recoverable (after about 2

TABLE 3

Seasonal variations in bacterial numbers and environmental factors in the A_1 horizon (6 cm depth). Counts expressed in millions per g. oven dry soil

Date	pH	% moisture content*	% organic carbon content	Loss on ignition (%)	Number of bacteria
November 1966	5.00	33.5	3.5	8.8	3.70
December	4.64	30.8	19.1	33.6	9.92
January 1967	4.16	—	3.6	8.2	1.79
February	5.39	33.5	5.2	11.7	2.17
March	5.19	37.5	4.6	10.7	5.49
April	6.51	28.9	2.8	7.0	2.18
May	6.15	38.1	5.0	11.8	9.26
June	5.34	25.4	2.9	8.2	2.39
July	4.70	23.4	3.9	8.9	1.69
August	4.31	25.8	3.5	7.8	12.0
September	5.21	34.0	4.5	9.9	9.85
October	5.67	37.0	6.3	10.7	5.82
November	5.25	30.5	3.0	8.6	7.39
January 1968	5.28	31.0	3.2	8.0	4.47
February	4.39	28.4	3'0	8.8	4.07
March	5.57	35.2	5.2	12.3	6.70
April	5.42	28.3	2.8	7.9	
May	5.32	35.4	3.7	9.4	11.6
June	4.14	33.1	—	—	3.32
July	5.20	33.9	—	—	11.2
August	4.56	19.8	—	—	5.41
September	5.15	28.0	—	—	3.67

Mean no. of bacteria for 1967 5.45 Standard Deviation 3.72
Mean no. of bacteria for 1968 6.26 Standard Deviation 3.10

* Moisture contents are expressed as a percentage of the wet weight of the soil.

months). Although decomposition was not complete at this stage, earthworm activity caused the removal of the last remaining leaf fragments. During the first 3 days of the decomposition period, numbers rose ten-fold, and almost 3-fold after a further 4 days. After 1 to 2 weeks, the population level began to fall. (Table 5).

Oak litter. In comparison with the ash litter, the establishment of bacterial populations was very slow. Practically no increase in population size occurred during the first two months ,but after this a gradual increase in numbers occured for the next ten months, at which time counting was discontinued. Appreciable quantities of leaf litter remained on the ground after 12 months (Table 6).

TABLE 4

Seasonal variations in bacterial numbers and environmental factors in the $O_h + A_h$ layer. Counts expressed in millions per g. oven dry soil

Date	pH	% moisture content*	% organic carbon content	Loss on ignition (%)	Number of bacteria
November 1966	5.85	53.7	—	—	27.5
December	4.10	66.8	16.7	34.1	71.8
January 1967	5.43	—	—	—	30.1
February	5.50	53.7	9.6	22.8	9.25
March	5.42	59.7	14.9	27.6	34.0
April	7.46	49.1	8.7	18.1	11.3
May	6.42	51.4	13.4	24.2	89.6
June	5.94	45.1	—	19.0	18.0
July	5.35	36.0	14.9	25.8	6.25
August	4.69	44.1	8.0	16.2	25.3
September	6.45	56.5	9.5	19.4	37.2
October	6.11	61.7	16.5	36.1	36.4
November	5.63	50.1	5.1	11.9	15.4
December	5.42	56.3	8.5	17.8	50.2
January 1968	5.84	56.8	7.6	16.8	108.2
February	5.40	52.1	9.0	19.8	30.2
March	5.44	49.6	9.2	21.2	15.3
April	5.72	50.6	—	15.2	22.4
May	5.02	49.0	6.2	14.8	6.2
June	4.77	47.3	—	—	20.2
July	5.02	39.9	—	—	12.9
August	4.68	24.0	—	—	68.7
September	5.17	39.7	—	—	25.2

Mean no. of bacteria for 1967 30.25 Standard Deviation 22·05
Mean no. of bacteria for 1968 34.37 Standard Deviation 32.96

* Moisture contents are expressed as a percentage of the wet weight of the soil.

TABLE 5

Seasonal variations in bacterial numbers on decomposing ash litter Counts expressed in millions per g. oven dry leaf litter

Age of litter	Number of bacteria		
	1966/7	1967/8	1968/9
Initial count	0.003	59.1	51.1
3 days	—	561	130
1 week	—	1 625	222
2 weeks	—	2 040	108
4 weeks	301	800	—
8 weeks	312	1 210	—

TABLE 6

Seasonal variations in bacterial numbers in decomposing oak litter
Counts expressed in millions per g. oven dry leaf litter

Date	Age of litter (months)*	Number of bacteria	
		1966/7	1967/8
November	0	1.68	3.64
	½	—	10.32
December	1	1.56	—
January	2	1.56	0.94
February	3	25.0	178
March	4	22.7	5.61
April	5	5.35	7.01
May	6	25.0	9.85
June	7	87.8	348
July	8	5.36	282
August	9	47.6	152
September	10	66.1	1 220
October	11	74.0	—
November	12	44.1	—

* Period during which bagged litter has lain on ground.

TABLE 7

Average cell dry weight for each group of isolates

Group		Cell weight $\times 10^{-13}$ g
1	*Achromobacter* (?)	3.66
2a	*Arthrobacter*	4.61
2b	*Arthrobacter*	5.69
3	*Arthrobacter*	2.11
4a	*Bacillus megaterium/cereus*	47.6
$4b_1$	*Bacillus cereus/mycoides*	48.2
$4b_2$	*Bacillus circulans/laterosporus/brevis*	67.5
4c	*Bacillus* spp	17.9
4d	*Bacillus subtilis*	8.42
$4e_1$	*Bacillus circulans*	10.0
$4e_2$	*Bacillus circulans*	20.1
6	*Mycobacterium*	1.66
7a	*Pseudomonas* group II	6.51
7b	*Pseudomonas* group I	3.83
7c	*Pseudomonas* group II	1.96
$7d_1$	*Paracolon* group	7.12
$7d_2$	*Coli-aerogenes* group	5.84

Biomass estimations.

The cell dry weights of isolates in each of the main taxonomic groups of bacteria found on the site are given in Table 7. These figures were used to calculate the biomass of each group of organisms and the total bacterial populations in the ecosystem (Table 8). The estimates for the humus layer

TABLE 8

Biomass estimates for each group and habitat (g. dry wt. per hectare)

Group and Genus	Ash litter	Oak litter	H horizon	Mineral soil	TOTAL
1 *Achromobacter*	3.71	—	60.0	113	182.7
2a *Arthrobacter*	16.56	0.57	—	—	17.1
2b *Arthrobacter*	11.54	0.35	—	—	11.9
3 *Arthrobacter*	7.27	—	—	—	7.3
4a *Bacillus*	—	2.96	213.4	13 252	13 468
$4b_1$ *Bacillus*	—	—	215.8	7 457	7 673
$4b_2$ *Bacillus*	—	—	150.9	6 264	6 415
4c *Bacillus*	—	—	40.1	2 766	2 806
4d *Bacillus*	8.53	—	9.4	—	17.9
$4e_1$ *Bacillus*	2.04	—	—	1 085	1 087
$4e_2$ *Bacillus*	—	—	—	1 554	1 554
6 *Mycobacterium*	—	—	13.0	25	38
7a *Pseudomonas*	23.75	—	—	—	24
7b *Pseudomonas*	3.87	4.40	8.3	—	17
7c *Pseudomonas*	—	—	10.6	92	103
$7d_1$ Paracolon group	4.34	1.33	—	—	6
$7d_2$ *Coli/aerogenes*	—	2.72	—	—	3
8 *Staphylococcus*	2.56	0.26	4.7	64	72
Unclassified	7.38	1.80	172.1	2 306	2 487
Total	91.56	14.39	904.3	34 980	35 990

and the mineral soil are based on the average of the counts made in the study of seasonal variations (3.35×10^7 and 5.95×10^6 per g respectively). The figures for the litter bacteria are based on an average of the seasonal counts (excluding the initial counts) and the average amounts of litter remaining throughout the year. The peak annual biomasses for litter bacteria will be rather higher than these. The total bacterial biomass estimated in this way is approximately 35.99 kg/ha for the habitats investigated.

DISCUSSION

The difference in the rates of decomposition of oak and ash litter at Meathop Wood is reflected both in the maximum levels for the bacterial

populations and the rapidity with which these levels are reached. The different maxima agree with previous reports that in temperate broad-leaved forests, ash litter supports among the highest bacterial populations and oak litter some of the lowest (EGOROVA, ENIKEEVA and BOL'SHAKOVA, 1964). A possible explanation for these differences lies in the reaction of the two litter types. Whereas ash litter at Meathop Wood has a pH of 6.1-6.4 while on the soil surface, oak litter has a pH of 4.5-4.9 during the first 12 months of decomposition (BAILEY, pers. comm.). A further factor which may inhibit bacterial growth on oak litter is the high tannin content and this is supported by the fact that the initial rise in the oak litter population coincides with removal of tannins by leaching and decomposition (GILBERT and BOCOCK, 1960).

The population changes observed for bacteria on the oak litter at Meathop Wood differ markedly from the figures obtained by MINDERMAN and DANIELS (1967) for an oak forest in Holland. They found that a peak population of 20×10^9 cells per g. organic dry matter was reached within a few days of the leaves reaching the ground and becoming moistened in October, and that the count then declined to a level of $2\text{-}3 \times 10^9$ cells per g organic dry matter, remaining steady from February to June. However, Minderman and Daniels used a direct counting technique and their litter was collected after an exceptionally dry summer, so their results cannot be compared simply with the figures given in the present paper.

The main feature to emerge from the estimates of biomass for the individual groups of bacteria is the dominance of the genus *Bacillus* which accounted for 91.8 % of the total biomass in all habitats and 92.5 % of the mineral soil population (Table 9). Because of the comparatively large size of most bacilli, this dominance is much more apparent when populations are expressed in terms of biomass than when expressed numerically (HISSETT & GRAY, 1973). However, members of this genus may be present as spores and may not contribute as much to soil metabolism as their abundance implies. On leaf litter, the main genera are *Pseudomonas* and *Arthrobacter*,

TABLE 9

Dominant genera as a percentage of the biomass in each habitat

Genus	Groups	Habitat				Total
		Ash litter	Oak litter	Oh + Ah layer	Mineral soil	
Achromobacter	1	4.1	0	7.3	0.3	0.5
Arthrobacter	2 & 3	38.6	6.5	0	0	0.1
Bacillus	4	11.5	20.6	69.5	92.5	91.8
Mycobacterium	6	0	0	1.4	0.1	0.1
Pseudomonas	7a, b, c	30.2	30.6	2.1	0.3	0.4
*Enterobacteriaceae**	7d	4.7	28.2	0	0	0.03
Staphylococcus	8	8.1	12.5	0.5	0.2	0.2

* The Enterobacteriaceae were mainly found on the fresh litter, so may not be part of the normal decomposer population.

the latter being less abundant on oak litter. This confirms the earlier impression gained from merely counting the cells (HISSETT and GRAY, 1973).

The estimate of bacterial biomass can be used in conjunction with the substrate input to the soil to estimate the probable maximum growth rate of bacteria in the ecosystems (GRAY and WILLIAMS, 1971). Substrate requirements for maintenance and growth are linked by the following equation (MARR, NILSON and CLARK, 1963).

$$\frac{dx}{dt} + ax = Y \frac{ds}{dt}$$

where a = specific maintenance constant (hr^{-1}), x = biomass of cells (g), s = the substrate available (g) and Y = the yield coefficient (g bacteria produced per g substrate utilised).

BABIUK and PAUL (1970) have suggested that for soil bacteria, a suitable value for a would be 0.001 hr^{-1} and for Y, 0.35. Estimates of the biomass of bacteria and the rate of substrate input are given in Table 10. The biomass of the bacteria has been arrived at by applying corrections to the value obtained for the oak and ash litters, the humus and the soil. It has been assumed that the amount of bacteria on the other litter and organic matter inputs is the same as the average for the oak and ash litters i.e. 0.22 g bacteria per kg litter. Thus the biomass of bacteria for the whole soil and litter complex is 36.87 kg per hectare. Similar corrections have been applied to the litter input figures to include the root production (SATCHELL, 1970); HIBBERD, pers. comm.) and root exudates (GRAY and WILLIAMS, 1971). This gives a figure of 7061 kg organic matter input per year per hectare. These figures differ from the provisional estimates published by GRAY and WILLIAMS (1971) because of newer information on the amount of mineral soil present on the site, and may need to be refined again later.

TABLE 10

Estimates of bacterial biomass and rate of litter input in the experimental site

Bacterial biomass for habitats investigated	35.99 kg
Estimated bacterial biomass for other leaf litters	0.360 kg
Estimated bacterial biomass on twigs, etc.	0.520 kg
Total bacterial biomass	36.87 kg
Annual input of litter measured (Hissett and Gray, 1973)	5446 kg
Estimate of annual root litter production	928 kg
Estimate of annual root exudate production	687 kg
Total annual organic matter input	7061 kg

Using these figures, it appears that 923 kg of substrate per year are required for maintenance of the bacterial population. If it is assumed that the remainder of the substrate is used for bacterial growth and that there is no fungal or animal growth, then the bacteria would have an average generation time of 4.07 days. If it is assumed that fungal and animal activity do take place and that not more than 40 % of the substrate is available to bacteria, the minimum generation time would be 10.2 days.

The implication of these calculations is that growth of soil organisms is either very slow, compared with that encountered in the laboratory, or occurs rapidly for very short periods of time. This almost certainly accounts for the failure of most methods of direct observation to follow bacterial growth in the soil, since the event to be observed is comparatively rare. A further problem is encountered if similar calculations are made for soil fungi, for here estimates of maintenance requirements for the hyphae measured by the agar-film technique (JONES and MOLLISON, 1948) suggest that more energy is required for maintenance than the input would provide (GRAY & WILLIAMS, 1971). It is probable that the agar-film technique vastly overestimates the living fungal population of soil and litter even when only stained hyphae are measured. Therefore, until more reliable methods are used for measuring fungal biomass, calculations of the energy flow through soil microbial populations are likely to be inaccurate. Such calculations are to be published shortly (FRANKLAND, pers. comm.).

SUMMARY

The bacterial populations of oak and ash litter and soil from a deciduous woodland have been compared by counting techniques and by the calculation of the biomass of individual bacterial types. The predominance of *Bacillus* in all environments has been established. Calculations of the growth rates of bacteria, based on these biomass figures, suggest that the growth rates are very slow, with a minimum generation time of 4.07 days.

ACKNOWLEDGEMENTS

We wish to thank the Natural Environment Research Council for a grant which enabled us to start the work described in this paper. We also wish to thank Dr. J. E. SATCHELL, Dr. J. FRANKLAND, Mr. J. HIBBERD and Mr. A. D. BAILEY for useful discussions and for data relating to the soil and site characteristics.

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